Thermal-tactile integration in object temperature perception

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Thermal-tactile Integration in Object Temperature Perception

Hsin-Ni Ho, Hiu Mei Chow, Sayaka Tsunokake, Warrick Roseboom

Abstract— The brain consistently faces a challenge of whether and how to combine the available information sources to estimate the properties of an object explored by hand. While object perception is an inference process involving multisensory inputs, thermal referral (TR) is an illusion demonstrating how interaction between thermal and tactile systems can lead to deviations from physical reality – When observers touch three stimulators simultaneously with the middle three fingers of one hand but only the outer two stimulators are heated (or cooled), thermal uniformity is perceived across three fingers. Here we used TR of warmth to examine the thermal-tactile interaction in object temperature perception. We show that TR is consistent with precision-weighted averaging of thermal sensation across tactile locations. Further, we show that prolonged contact with TR stimulation results in adaptation to the local variations of veridical temperatures instead of the thermal uniformity perceived across three fingers. Our results illuminate the flexibility of processing that underlies thermal-tactile interactions and serve as a basis for thermal display design.

Index Terms—Thermal perception, object perception, human information processing, perception and psychophysics

1 Introduction

DIRECT manual exploration is an intuitive and reliable way to obtain thermal and mechanical information about objects that is unavailable to other sensory modalities [1]. This information is key to recognizing the material composition of the objects - consider the coolness and hardness of metal or the warmness and softness of fabrics [2]. However, studies have shown that our tactual object perception is not always veridical [3]. Interaction between thermal and tactile systems can lead to deviations from physical reality in object perception. Thermal referral (TR) is such an illusion of object temperature perception [4]. This illusion was first demonstrated in an experiment wherein the middle three fingers of one hand made contact with three thermal stimulators. When the outer two stimulators were warm (cold) and the center stimulator was thermally neutral, warmth (cold) was felt at all three fingers. Notably, this referral of thermal sensation disappeared when the middle finger was withdrawn from the central (neutral) stimulator, indicating that congruent tactile stimulation is essential for TR to occur [4].

While TR reflects the diffuse nature of the thermoceptive system [5,6,7], its similarities to perceptual filling-in in terms of perceptual continuity and feature averaging [8] and its facilitative role in object perception point to the possibility that TR might involve inference processes related to object perception. Previous work has shown that inferences regarding visual properties change haptic estimates, such as temperature, weight, surface texture and size [9,10,11,12]. Thus, it is possible that TR involves a cognitive mechanism that assumes homogenous object properties at different points of contact, compensating for the discontinuities in the thermal perception to create a coherent perceptual experience across thermal and tactile modalities. In essence, TR is a phenomenon that reflects how thermal and tactile modalities coordinate to resolve incoherent spatial information in object perception. This thermal-tactile interaction has a significant implication in the development of haptic interfaces incorporating both thermal and tactile feedback. For example, TR has been used to present thermal feedback at the fingerpad through thermal stimulation at the finger side [13]. This technique allows the fingerpad to be free from direct contact with a thermal stimulator. Such a display can be easily integrated with other haptic devices, such as vibrators and electrotactile displays, to create a holistic image of a virtual object.

To advance our knowledge regarding object perception and to facilitate development of haptic interfaces, in this study we used TR to investigate the thermal-tactile inter-

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action in object temperature perception. We aimed to understand how thermal information from each tactile location contributed to a global percept of uniformity seen in TR (Experiment 1) and whether prolonged contact with the TR stimulation would result in adaptation to the local variations of veridical temperatures or the thermal uniformity perceived across three fingers (Experiment 2). In Experiment 1, we investigated the combination of thermal information across fingers under TR with a linear averaging model and precision-weighted Bayesian cue combination model, which is a common approach used to describe how different sources of perceptual information are combined [10,14,15,16]. In Experiment 2, we investigated how prolonged contact with TR affects the perception of subseqent thermal stimulation. It is known that continuous exposure to a stimulus would result in adaptation, i.e. changes in the response characteristics of neurons to stimulation with time [17]. Adaptation has been referred to as the psychophysicists' microelectrode because there is often a strict contingency between adaptation and changes in perception [18,19,20]. The perceptual "aftereffects" of the adaptation can provide clues as to how our senses encode and represent the stimulus [19,20,21,22]. Accordingly, by examining the thermal referral aftereffect, it is possible to elucidate the perceptual coding structure that underlies TR in particular, but thermal-tactile interactions more generally.

2 Materials and Methods

2.1 Participants

Eleven naïve paid volunteers (two males and nine females) and two authors HH (female) and ST (female) participated in Experiment 1. The participatns aged between 22 and 44 years and the mean ± SD of the participant group ages is 35.2 ± 7.4. Eleven naıve paid volunteers (three males and eight females) and three authors HH (female), DC (female) and WR (male) participated in Experiment 2. The participants aged between 24 and 45 years and the mean ± SD of the participant group ages is 34.5 ± 5.6. Five participants (one male and 4 females), including the author HH (female), were common to both experiments. There was more than one-year interval between Experiments 1 & 2, so we assumed the influence from reuse of these participatns woud be limited. The female participants outnumbered the male participants due to the gender unbalance in the the pool of participant recruitment. It has previously been reported that females are in general more sensitive to tactile stimulations [23]. All the participants were right-handed, except ST in Experiment 1. The participants had no known abnormalities of their tactile and thermal sensory systems. Recruitment of participants and experimental procedures were conducted in accordance with the Declaration of Helsinki.

2.2 Apparatus

Experiments 1 and 2 are conducted with the same set of experimental apparatus (Fig. 1). To adapt both participants' hands to a preset temperature, two thermal displays – hereafter, termed adapting thermal displays - were used.

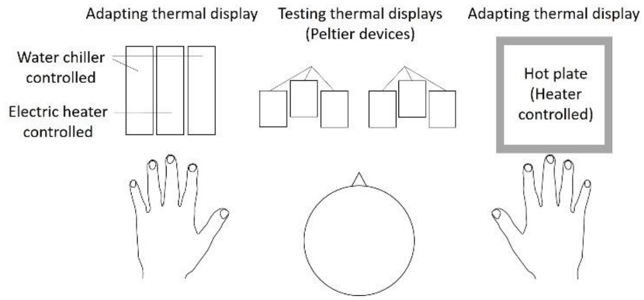

Fig. 1. Experimental thermal apparatus set up for this study. The adapting thermal displays at two sides were used to adapt both participants' hands to a preset temperature. After adaptation, the participants moved their hands to the testing thermal displays to feel the test thermal stimulation applied to the middle three fingers of each hand.

A custom made hot plate (180 x 180mm) consisting of heating wire (Yagami Inc, Nagoya, Japan) and copper plate was used for reference (dominant) hand adaptation, and a thermal display made of three copper bars, two of which controlled by a water-heating/cooling system (Eyela NCB-1200, Tokyo Rikakikai Co. Ltd, Tokyo, Japan) and one of which by electric heater (Takagi Mfg. Co., Ltd., Tsukuba, Japan), was used for test (non-dominant) hand adaptation. The two adapting thermal displays were put near each hand respectively. In between the adapting thermal displays, another two thermal displays –hereafter, termed testing thermal displays - were used to present test thermal stimulation to the middle three fingers of each hand. Each thermal display consisted of three Peltier devices with a surface area of 20 x 20 mm (FPH1-7106M, Fujitaka Co., Kyoto, Japan). The Peltier devices were housed in plastic holders, which expose a constant surface area of 300 mm^2 of the Peltier devices to the participant's fingerpad. Two digital–analog converters (ADI16-16 and DA16-16, Contect Co., Osaka, Japan) and a PI control loop programmed in Matlab (Mathworks, Inc., MA, USA) were employed to control the surface temperatures of the Peltier devices. The temperature feedback was provided by thermistors (457 μm in diameter and 3.18 mm in length; 56A1002-C8, Alpha Technics, CA) sandwiched between the Peltier devices and plastic holders. With this configuration, the thermistors didn't make contact with the skin directly. The maximum rate of temperature change was 10ºC/sec for cooling and 18ºC/sec for heating. Achieving a steady state took about 1 sec. After a steady state had been reached, the temperature of each Peltier device could be maintained within 0.5ºC of the desired temperature. To facilitate heat dissipation, the testing thermal displays were placed on top of copper heat sinks (P-200S, Takagi Mfg. Co., Tsukuba, Japan) connected to a water-cooling system (Eyela NCB-1200, Tokyo Rikakikai Co. Ltd, Tokyo, Japan).

2.3 Experimental design and statistical analysis

2.3.1 Thermal referral stimulation

Thermal referral (TR) occurs with both warm and cold stimulations and has been demonstrated across the fingers and the forearm. The effect of TR is in general stronger under warm than cold stimulation (in terms of people's ability to distinguish the illusory thermal sesation from the veridical thermal senation) [24,25]. The difference between warm and cold referral presumably reflects a fundamental difference between our senses of warmth and cold. Our sense of warmth has been shown to be more diffuse than our sense of cold [26,27], and the spatial summation is greater for warm stimuli than for cold stimuli [28]. TR can be demonstrated with 3 stimulated sites, e.g. [warm, neutral, warm], as well as with only 2 stimulated sites, e.g. [warm, neutral], and the effect of TR redcues with increasing somatotopic distance among the stimulated sites [24,25]. In this study, we used warm referral, with the classical 3 finger configuration. This configuration has been shown to be able to give illusory thermal uniformity across 3 fingers (strongest effect possible) for both warm and cold referrals [29].

2.3.2 General procedure

In this study, the experiments were conducted in a climate room whose temperature and humidity were set at 25°C and 30%, respectively. The neutral skin temperature, i.e. the temeprature that does not feel either warm or cold, was set at 33°C [30]. In all conditions in Experiments 1 & 2, the test and reference hands were tested simultaneously. The test hand is the non-dominant hand and the reference hand is the dominant hand of each participant. Non-dominant hand was used as the test hand because we would like to exclude the influence from the difference in dexterity of the dominant hands among participants. A single interval forced choice procedure was adopted, in which the participants were instructed to report which hand (right or left) felt warmer. Five levels of stimulus temperature were used in all conditions in Experiments 1 & 2 (Please refer to Sections 3.1 and 4.1 for more infromation about the temperature levels). Each stimulus temperature was repeated 12 times, giving a block of 60 trials that were presented in randomized order. There were three blocks in each condition, which gave a total of 180 trials. Each block of trials lasted for about 30 min, and there was at least a 20-min break between the blocks.

2.3.3 Statistical analysis

Each participant's data were fitted with a *cumulative Gaussian* function [31]. The mean of the fitted function was used as an estimate for the Point of Subjective Equality (PSE) between two hands while the standard deviation indicates the precision with which the participant made the categorization of relative warmness (coolness). Participants who had a standard deviation more than three times that of the group mean were excluded from further analysis because this high variability in the responses indicated that they could not easily discriminate which hand was warmer for the range of thermal differences presented. Following this exclusion criteria, 11 participants in Experiment 1 and 10 participants in Experiment 2 remained.

Bayesian statistics were used to analyze the data from Experiments 1 & 2 with JASP [32]. The Bayesian Paired Samples T Tests were conducted with the default Cauchy prior. In Bayesian tests, the Bayes factor, BF_{10}, indicated the relative strength of evidence for an alternative hypothesis to the null hypothesis. A Bayes factor of 1/3 or less is commonly taken as evidence for the null hypothesis and of 3 or more as substantial evidence against the null [33]. Bayesian tests are in particular useful when non-significant results are obtained with traditional Frequentist tests because they provide an approach for discriminating whether non-significant results support a null hypothesis over a theory or whether the data are just insensitive.

3 Experiment 1: Combination of Thermal Information Across Fingers

The aim of this experiment was to understand how the thermal inputs from each finger were combined to reach a final percept global percept of uniformity seen in thermal referral. Here we used both a linear averaging model, in which the independent inputs are directly averaged, and a precision-weighted model, in which the independent inputs are combined based on a weighting proportional to the inverse of their variability. The latter model is a common approach used to describe how different sources of perceptual information are combined [10,14,15,16]. In the precision-weighted model, the independent estimates of D2, D3, and D4, $\hat{S}_{D2}, \hat{S}_{D3}$ *and* $\hat{S}_{D4}$, i.e. the PSEs of D2, D3, and D4, are combined based on a weighting proportional to the inverse of their variability [14]:

$$\hat{S}_{overall} = w_{D2}\hat{S}_{D2} + w_{D3}\hat{S}_{D3} + w_{D4}\hat{S}_{D4} \quad (1)$$

where w_{D2} is inversely proportional to their variances:

$$w_{D2} = \frac{1/\sigma_{D2}^2}{1/\sigma_{D2}^2+1/\sigma_{D3}^2+1/\sigma_{D4}^2} \quad (2)$$

and likewise for w_{D3} and w_{D4}. Accordingly, the less variable the estimate, the higher the weighting would be in combination. In other words, when combining multiple estimates of the same property, more trust is given to the more reliable information source.

To conduct this analysis, we measured the thermal perception, and variability in thermal perception, for each finger individually and altogether under TR stimulation. We then compared the obtained results for the TR condition with what we would predict under a linear averaging and a precision-weighted model based on the thermal perception for each finger alone.

3.1 Procedure

In the experiment TR stimulation was set at [37, 33, 37] ˚C for D2, D3 and D4, respectively. Note that D3 was thermally neutral because it was in contact with the neutral temperature of 33 ˚C. The sensory variability of D2, D3 and D4 and three fingers all together were measured in separate experimental sessions, conducted in a pseudo-randomized order. At the beginning of each experimental session, both hands were initially adapted to neutral temperature of 33˚C for 10 minutes. Upon hearing a sound cue, participants moved their hands to the test thermal displays. When testing individual fingers (D2, D3 or D4), the

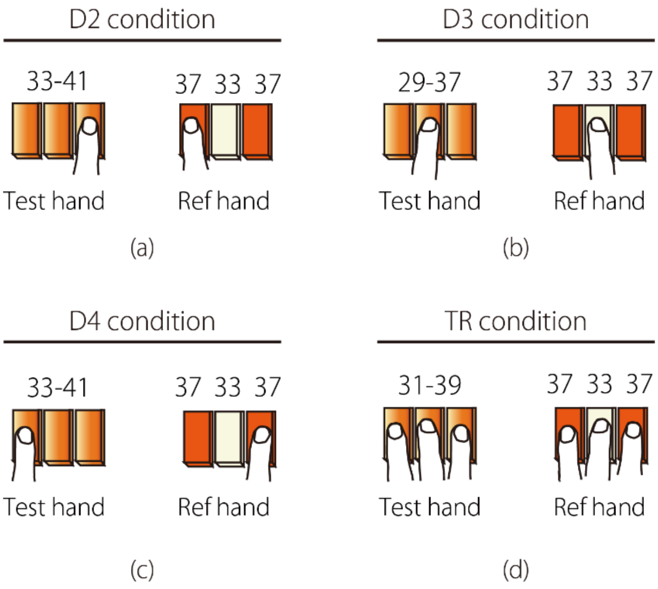

Fig. 2. Experimental conditions in Experiment 1. Here we measured the perceptual estimate and variability of thermal sensation for fingers individually and altogether under TR stimulation. We used a two hand configuration and both hands were initially adapted to the neutral temperature of 33˚C. In the test phase, the test hand touched a thermal stimulus that varied in a range between 29-41 ºC and the reference hand touched the TR stimulation. We asked participants to compare the thermal sensations between two hands for each finger individually (a-c), or in combination for thermal stimulation that would produce TR illusion (d).

TABLE 1
PSES AND SDS FOR TEMPERATURE ESTIMATION AT EACH FINGER AND 3 FINGERS AS A WHOLE UNDER TR STIMULATION. SHADED PARTICIPANTS ARE THOSE WHOSE SD FOR MEASURED TR WAS SMALLER THAN THE SMALLEST SD OF D2, D3 OR D4. UNITS IN DEGREES CELSIUS.

	SD				PSE			
Participant	D2	D3	D4	TR	D2 (37)	D3 (33)	D4 (37)	TR
1	1.5	2.3	1	1	37.9	33.5	38.1	36.3
2	2	0.9	4.2	1.6	35.5	32	37.7	34.5
3	1.1	0.3	0.4	0.9	36.6	32.7	37.1	36.3
4	3.3	1.3	0.3	1.1	35.7	30.7	35.1	34.3
5	3.1	2.4	2.8	1.8	39.4	32.7	38.3	37
6	1.5	1	1.4	1.3	38.1	32.4	36.9	36
7	1.4	1.3	2	1.1	36.3	33.7	36.9	34.9
8	0.2	1	1.7	0.4	37.1	32.8	39.7	35.1
9	0.9	1	1	0.2	35.9	31.5	37.2	35.9
10	1.7	1.7	3.3	0.7	36.8	32.6	38.8	35.6
11	1.2	1.1	2	1.1	37.1	34	38.3	35.8
mean±SE	1.6±0.3	1.3±0.2	1.8±0.4	1.0±0.1	36.9±0.4	32.6±0.3	37.6±0.4	35.6±0.2

finger of the reference (dominant) hand touched the corresponding temperature stimulation (D2 and D4 to 37˚C, D3 to 33˚C), and the finger of the test (non-dominant) hand touched the three-stimulator thermal display, in which the temperature of the corresponding stimulator varied between 33, 35, 37, 39, 41˚C for D2 and D4 and 29, 31, 33, 35, 37 ˚C for D3 between trials (Fig. 2a-c).When testing three fingers all together, the reference (dominant) hand touched the TR stimulation, and the test (non-dominant) hand touched the three-stimulator thermal display, in which the temperatures varied between 31, 33, 35, 37, 39 ˚C (same across 3 channels) between trials (Fig. 2d). Another sound cue was presented after 5s to cue participants to lift both hands off the thermal display and report which hand (left or right) feels warmer by pressing left and right arrow keys of the keyboard. The participants placed both of their hands back on the adapting thermal displays after giving their response and the next trial started after a 10s re-adaptation period. Note that the stimulus temperature range was chosen according to the temperature presented to the reference hand in each condition. For example, in D3 condition (Fig. 2b), we used 33 ˚C as the center stimulus temperature and had two temperature levels lower and higher than the center stimulus temperature in a 2 ˚C step to make 5 levels of stimulus temperature. Each participant's data were fit ted with a cumulative Gaussian function. The PSE told us the apparent intensity of TR stimulation and the standard deviation informed us the sensory variability in the estimation.

3.2 Results & Discussion

The PSEs and SDs for D2, D3 and D4 individually and altogether are listed in Table 1. The results of PSEs agree with the previous findings that the illusory thermal sensation perceived at D3 is not simply a "copy" of the thermal sensation elicited by the thermal changes applied to D2 and D4 [29,34]. This is because, if it were the case, the PSE of TR would be similar to those of D2 and D4. The results listed in Table 1 show clearly that this was not the case, as the PSEs of TR were *lower* than those of D2 and D4 and *higher* than that of D3 for all participants, indicating an averaging process is involved to combine the thermal changes applied to the three fingers.

Looking at the performance of the precision weighted model estimates, based on the single finger participant estimates, we see that it does a good job of describing the participants' reports under the three-finger TR condition (see Figure 3b, Bayesian Paired Samples T-Test: BF_{10} = 0.37). While the precision-weighted model estimates are broadly consistent with the obtained TR results, the linear averaging also produced estimates largely consistent with participants' reports under TR (Bayesian Paired Samples T-Test: BF_{10} = 0.34). These comparisons between the measured TR to the estimates produced by precision weighted model and linear averaging model did not provide strong support for either precision weighted or linear estimates over each other. That our data do not strongly support one combination rule or the other is probably due to the fact that the precision of temperature estimation was similar among three fingers (see Table 1) – conditions that approximate linear averaging under the precision weighted scheme. A strong prediction that might differentiate the precision-weighted, *Bayesian* model from linear averaging model is that the precision-weighted model also specifies

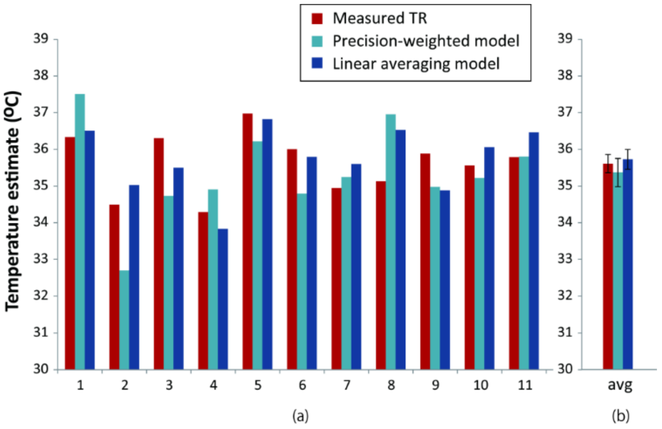

Fig. 3. Comparison of actual and predicted apparent temperatures for TR stimulation. (a) Measured TR (red bars), the precision weighted model estimates (light blue bars) and the linear averaging model estimates (dark blue bars) for 11 participants. The measured TR is the Point of Subjective Equality (PSE) obtained in TR condition (see Fig. 2d). The precision weighted model estimates were calculated according to (1) and (2). The linear averaging model estimates were calculated by directly averaging the PSEs of D2, D3 and D4 (see Table 1). (B) Averages of all 11 participants. Both precision weighted model estimates and linear averaging model estimates are broadly consistent with the measured TR results. The errorbars indicate the standard error of the means.

that the overall precision of the combined estimate is better than the best precision of any single contributing estimate (i.e. the variability of the estimate in the TR condition should be lower than that obtained in any of the single finger conditions). Examining participants' reports, we find evidence that this is true when looking at the group mean SD (TR: Mean SD = 1.0; D2: mean SD = 1.6; D3 = mean SD= 1.3; D4: mean SD = 1.8; see Table 1); however, when looking at the individual data, only 4/11 of the participants fulfilled this requirement (shaded participants in Table 1). Overall, these results indicate that a simple averaging scheme (either precision-weighted or linear) is used for the integration of thermal information across three fingers to produce the TR illusion.

4 Experiment 2: Adaptation to Illusory Thermal Uniformity

The purpose of this experiment is to investigate how prolonged contact with TR affects the perception of subseqent thermal stimulation. In the experiment, the participants were adapted to the classical 3-finger configuration of TR (TR stimulation), a perceptually equivalent uniform stimulation across three fingers (physically uniform), or the physical temperatures presented in TR stimulation presented to each individual finger separately (physical temp). Here the physically uniform stimulation and the individual physical temperatures represent two bounds of possible outcomes of TR stimulation adaptation, with the physically uniform stimulation giving an aftereffect more like having adapted to the perceptual value of TR (i.e. illusion) and the physical temperature giving an aftereffect more like having adapted to the physical values of TR. By examining the thermal referral aftereffect, it is possible to elucidate the perceptual coding structure that underlies TR in particular, but thermal-tactile interactions more generally.

4.1 Procedure

4.1.1 Matching experiment

As there are individual differences in experiencing the thermal referral illusion [29], before the main adaptation experiment, each participant completed a matching experiment. This experiment aimed to find the temperature D2 and D4 should touch (T˚C) such that, when presented in combination with the middle finger touching neutral temperature at 33˚C, a thermal referral percept that is perceptually indistinguishable from a uniform presentation of 35˚C across all fingers was generated. Note that 35 ºC was chosen because (1) it is warm given a baseline temperature of 33 ºC; (2) it can be fully adapted within the initial adaptation duration of 10 minutes [35]; and (3) the outer finger temperature (T˚C) that needed to induce an illusory thermal uniformity of 35 ºC is reported to be about 38-39 ºC [29], which is below pain threshold [36].

At the beginning of the experiment, participants placed both of their hands on the adapting thermal displays which were set at the neutral temperature of 33˚C for 10 minutes. Upon hearing a sound cue, participants moved their hands to the test thermal displays. Their reference (dominant) hand touched the uniform temperature at 35˚C, and test (non-dominant) hand touched the three-stimulator thermal display, in which the central stimulator was set at the neutral temperature of 33˚C and the temperature of the outer stimulator varied between 35, 37, 39, 41, 43˚C between trials. Another sound cue was presented after 5s to cue participants to lift both hands off the thermal display and report which hand (left or right) felt warmer by pressing left and right arrow keys of the keyboard. The participatns placed both of their hands back on the adapting thermal displays after giving the responses and the next trial started after a 10s re-adaptation period. Each participant's data were fitted with a *cumulative Gaussian* function. The PSE told us about the outer finger temperature of thermal referral stimulation that would be equivalent for a physical uniform temperature 35˚C for each participant. The outer finger temperature (T˚C) was found to be in the range of 35.8 - 38.7 ºC, with a group mean of 37.1 ºC. For each participant, their own outer finger temperature (T˚C) was used in the TR stimulation in the subsequent adaptation experiment.

4.1.2 Adaptation experiment

In the adaptation experiment, the aftereffect that we were looking at was the "new physiological zero" created after adaptation. Physiological zero refers to the temperature that feels thermally neutral. As there is no fixed reference point for temperature perception, one's "physiological zero" can be manipulated through adaptation [17]. The subsequent thermal perception (aftereffect) is referenced to

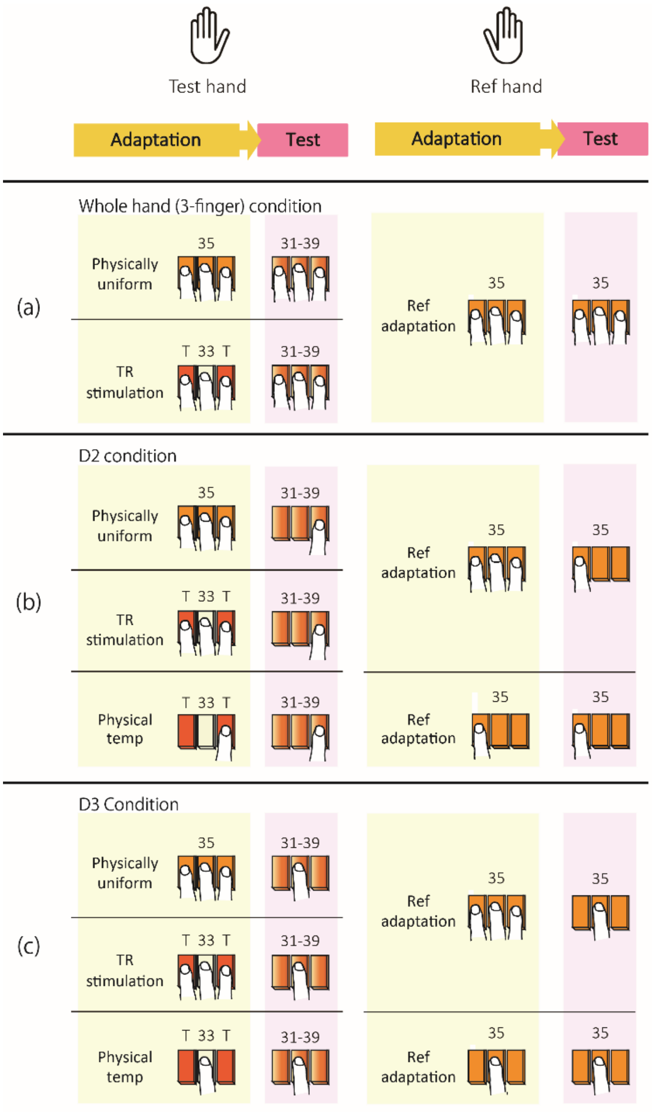

Fig. 4. Experimental conditions in Experiment 2. In this experiment, each participant's test hand was adapted to different patterns of temperature stimulation. At the same time, the participant's reference hand was adapted to the reference temperature of 35˚C. After adaptation, the participants touched a test stimulus varied between 31-39 ºC with their test hand and 35˚C with their reference hand. The participant's task was to report which hand felt warmer. From these data, we were able to estimate the "new physiological zero" for different adaptation conditions. To look at the effect as a whole and in relation to each individual finger, we manipulated the finger configuration in the adaptation and test phases. (A) The whole hand (3-finger) condition, wherein the middle three fingers of one hand were used in both adaptation and test phases. (B) D2 condition, wherein only D2 was used in the test phase. In the adaptation phase, the middle three fingers of one hand were used for physically uniform stimulation and TR stimulation and only D2 was used in physical temperature stimulation. (C) D3 condition, wherein only D3 was used in the test phase. In the adaptation phase, the middle three fingers of one hand were used for physically uniform stimulation and TR stimulation and only D3 was used in physical temperature stimulation.

this new physiological zero and a temperature above (below) which would be felt as warm (cold). A famous example is the "three-bowl illusion", wherein 27ºC water can feel either warm or cold depending on to which temperature the hand previously adapted [37]. To find the "new physiological zero" created after adaptation, we used two-hand configuration (Fig. 4). The participant's reference hand (dominant hand) was adapted to a reference temperature of 35ºC, and the participant's test hand (non-dominant hand) was adapted to one of the three adaptation conditions. After adaptation, the participants touched 35ºC with their reference hand, which elicited thermally neutral sensation because it is the same as the temperature of the reference adaptation, and a test stimulus varied between 31-39 ºC with their test hand. The participant's task was to report which hand felt warmer. We fitted these data with a psychometric function to estimate the "new physiological zero" for different adaptation conditions.

To look at the effect as a whole and in relation to each individual finger, we manipulated the finger configuration in the adaptation and test phases. In the whole hand (3-finger) condition (Fig. 4a), the test hand (non-dominant hand) of participants was adapted to physically uniform stimulation and TR stimulation in different sessions. When adapting to physically uniform stimulation, participants touched the adapting thermal display which were all set to 35˚C. When adapting to TR stimulation, participants touched the adapting thermal display in which the temperature of the center stimulator was set to 33˚C, and the two outer stimulators were set at T˚C (which was the temperature matched for each participant in the macthing experiments). At the same time, the reference hand (dominant hand) of participants touched the hot plate set at 35˚C. The initial adaptation duration at the beginning of each session was 10 minutes to ensure adequate exposure to the adapting stimuli. Upon hearing a sound cue, participants moved all three fingers of both hands and touched the testing thermal displays. In this test phase, the test hand touched test stimuli varied between 31, 33, 35, 37, 39˚C (same across three channels), and for the reference hand always 35˚C to create neutral thermal sensation. Another beep sound (after 5s) was presented when participants lifted their hands off the testing thermal displays and used the arrow keys on the keyboard to indicate which hand (left or right) feels warmer. The participants placed both of their hands back on the adapting thermal displays after giving the responses and the next trial started after a 10s re-adaptation period.

To look at the effect for each individual finger, we also tested D2 and D3 separately after adapting to three different temperature patterns – Physically uniform stimulation, TR stimulation and physical temperature (Fig. 4b & 4c). The procedure of adapting to physically uniform stimulation and TR stimulation were identical to that of the three-finger condition, except that at the test phase, only one of the fingers (D2 or D3) of both hands touched the test thermal display (the other two fingers were lifted up during contact). In the physical temperature adaptation, D2 and

D3 adapted to their corresponding physical temperature separately (D2 to T ˚C and D3 to 33 ˚C). The procedure was similar to that of the other two conditions, except that at both adaptation and test phase, only one of the fingers (D2 or D3) of both hands touched the thermal displays. The thermal perception of D2 or D3 was tested individually in separate sessions and participants were told which finger was the test finger at the beginning of each session.

4.2 Results & Discussion

The results of Experiment 2 are shown in Fig. 5. Here we show that when observers reported about all three fingers together, the PSE following TR adaptation (Test 2) was nearly identical to that following adaptation to the subjectively matched physical thermal uniformity (Test 1), as shown by the Bayesian Paired Samples T-Test (Test 1 v.s. Test 2, BF_{10} = 0.31 see Fig. 5). This result indicates that adapting to TR produces an aftereffect commensurate with the perceived, rather than physical temperatures of the fingers.

However, when reporting each finger in isolation, a different pattern of results is seen. Here, the data show strong evidence that the PSE following the TR adaption (Test 4 for D2, or Test 7 for D3) was different from that of the subjectively matched physical thermal uniformity (Test 3 for D2 or Test 6 for D3), as shown by Bayesian Paired Samples T-Tests for D2 (Test 3 v.s. Test 4: BF_{10} = 22.01) and D3 (Test 6 v.s. Test 7: BF_{10} = 85.56), respectively. Additionally, our data indicate a trend towards the PSE following TR adaptation (Test 4 for D2 or Test 7 for D3) being the same as having adapted to the local finger by itself (Test 5 for D2 and Test 8 for D3). However, the evidence here is not strong enough to accept or reject the null hypothesis that the PSE of these two conditions are the same as shown by the Bayesian Paired Samples T-Test for D2 (Test 4 v.s. Test 5: BF_{10} = 0.71) and D3 (Test 7 v.s. Test 8: BF_{10} = 0.40; see Fig. 5). Overall, these results indicate that the aftereffect depended on the spatial configuration of the fingers in the test phase. When asking about the thermal perception of the whole hand (3-finger) participants' responses were like having adapted to the illusory rather than physical stimulation. In contrast, when asking about the individual finger perception, participants' reports were more like having adapted to the physical values.

One possible explanation is that adaptation effect depends on spatial contingency of the fingers. Similar to the McCollough effect, wherein color aftereffects are contingent on the presence of particular grating orientation [38], only in the presence of the correct spatial configuration of fingers (all three in contact with the thermal surface), we obtain a pattern of results consistent with the illusion adaptation. This explanation in turn implies that the physiological zero for tactual temperature estimation would depend on the consistency of finger configuration to a recent sensory history. This is, however, highly speculative as the resetting of the physiological zero for temperature perception has been shown to be a rather automatic process, relating to change in the temperature threshold for TRPM8 activation and responses in DRG neurons [39]. In line with

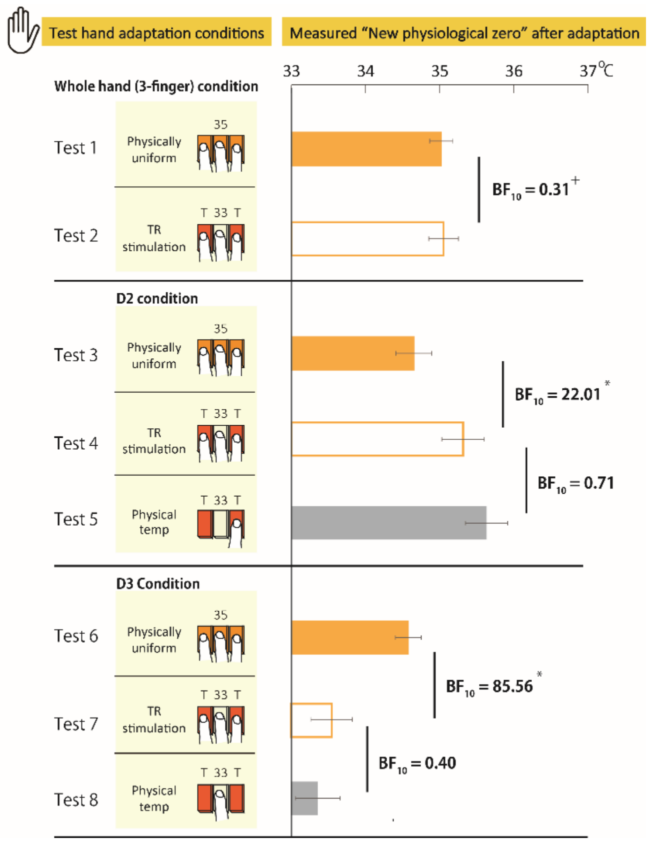

Fig. 5. Aftereffects of adapting to different thermal stimulation patterns under different configurations of fingers during testing (All fingers, D2, or D3 in isolation). Errorbars indicate standard error of means. The asterisk indicates substantial evidence against the null hypothesis (BF_{10} >3) and the plus sign indicates substantial evidence for the null hypothesis (BF_{10} < 1/3).

this view, our pattern of results may instead reflect a process that involves only peripheral adaptation, with adaptation to the illusory TR never occurring. Following only peripheral adaptation, such that each finger was adapted to a new physiological zero, presenting the 3-finger configuration in the test phase with a uniform testing thermal display would lead to different apparent temperatures across the 3 fingers. This inhomogeneous temperature distribution could lead to another TR-like temperature redistribution [4] – effectively the reverse TR to that presented in the adaptation period, with the thermal sensation for D2 and D4 being that of coolness, and the sensation for D3 being warm. If the sum of these thermal sensations is similar to 35^{o}C, we would find a matched PSE (see Test 2, see Fig. 5).

The apparent temperatures across 3 fingers under this situation can in fact be estimated based on our data, which showed that the physiological zeros of D2, D3 and D4 after adapting to TR stimulation were [35.3, 33.5, 35.3] ^{o}C (see Test 4 and Test 7 in Fig. 5), if we assume D4 would behave similarly as D2. The shift in apparent temperature as a result of the resetting of physiological zero can be estimated by the difference between the reference temperature, 35^{o}C, and the physiological zero of an adaptation pattern. This follows that the shift in apparent temperature of the three fingers would be [-0.3, 1.5, -0.3] ^{o}C. Based on this estimation, touching a test display of [35, 35, 35] ^{o}C after TR adaptation would give apparent temperatures of [34.7, 36.5, 34.7] ^{o}C across 3 fingers. In light of the results of Experiment 1 that the temperature integration across the 3 fingers follows of a simple averaging scheme, the overall apparent temperature would be 35.3 ^{o}C, which is indistinguishable from the reference temperature of 35 ^{o}C as the precision of temperature estimation is larger than 1^{o}C (see Table 1). Consequently, the whole hand adaptation effect (Test 2, Fig. 5) would be consistent with a peripheral only adaptation. In short, our data showed that prolonged contact with the TR stimulation resulted in adaptation to the local variations of veridical temperatures instead of the global uniform perception across 3 fingers. These findings indicate that adaptation of thermal perception occurs prior to integration of thermal information across tactile locations.

In the sensory processing hierarchy for object temperature perception, where does the thermal-tactile interaction that produces TR occur? It is known that tactile and thermal sensory systems have physiologically separate ascending sensory pathways [36] and that their representations in the brain occupy different cortical areas: Discriminative tactile sensations are mediated by the somatosensory cortex, whereas the haptic capacity of thermal sensations is subserved by the dorsal posterior insular cortex [40] and/or parietal–opercular (SII) cortex [41]. Convergence of thermal and tactile inputs at the subcortical level does exist, but TR is unlikely to occur at the spinal level as all the temperature specific neurons found in the superficial laminae of spinal dorsal horn, where thermoreceptors exclusively terminate, are insensitive to mechanical inputs [42,43]. In thalamus, some neurons have been found to be sensitive to both mechanical and cooling stimuli [44]. However, stimulation at these neurons did not elicit cold sensations. In brief, these neurophysiological findings suggest that TR, referral of thermal sensations to sites of tactile stimulation, is not merely a hard-wired process that involves subcortical thermoceptive pathway operations. Rather, TR likely results from crossmodal processing at cortical level.

5. General Discussion

Our results indicated that a simple averaging scheme (either Bayesian or linear) is used for the integration of thermal information across three fingers to produce a global percept of uniformity seen in TR and that adaptation takes place at a peripheral stage where information about temperature inputs are preserved for each finger and the thermal-tactile integration in TR occurs *after* this stage. On the basis of these findings, a possible underlying mechanism for TR is that it is driven by high-level crossmodal integration between thermal and tactile systems, and at the same time, subject to constraints posed by low-level organization of the thermoceptive pathway.

Touch plays a unique role in temperature perception. Dating back to 19th century, Weber proposed that touch serves to refer sensations of temperature produced by contact with an object *to the object* rather than *to the skin* (see [45]). In other words, touch signals the brain to switch from the interoceptive aspect (thermoregulation) to the exteroceptive aspect (object perception) of temperature perception during hand-object interactons. Our findings that the human brain uses strategies common to other sensory dimensions to infer the combined thermal properties across the hand further point to the possibility that the combination of different features in thermal-tactile perception follows inference processes for the purpose of coherent object perception. TR similarly could be driven by a mechanism in which inferences regarding tactile properties change temperature estimates. That is, the tactile modality signals a homogeneous surface, so the inference for the cause of the spatially incoherent thermal and tactile inputs is in favor of the hand touching a surface of a single, spatially coherent object, rather than a surface with different temperatures at sites in contact.

Meanwhile, TR is subject to constraints posed by low-level organization of the thermoceptive pathway. Thermal sensations are mediated by the small-fiber spinothalamic system, and the neurons on which the spinothalamic fibers terminate have huge receptive fields [5,6,7,40,46]. A thermally neutral site might also be activated if its receptive field overlaps with those being physically stimulated. This diffuse nature, and the tendency for the thermal sense to summate spatially separate inputs [47,48], would influence the temperature estimate of each site when multiple sites are in contact. This can be seen in our data that new physiological zeros following the TR adaptation (Test 4 and 7, Fig. 5) were not identical to those of the physical temperatures (Test 5 and 8, Fig. 5): The PSE of D3 was greater and the PSE of D2 was smaller than those of the corresponding physical temperatures. This constraint in neural organization explains why the amount of referral is in general lesser when referral occurs between only 2 adjacent fingers (i.e., between D2-D3 or D3-D4) or when D2 or D4 was the unstimulated finger and that TR can be diminished by increasing somatotopic, rather than spatial, distance between the stimulated sites [24,25]. Further investigation is required to determine whether the integration rule found in the present study generalizes to stimulation configurations that produce different magnitudes of referral (generally lesser) and further, whether it can also be applied to thermal integration across location in other parts of the body.

Haptic object perception is a highly flexible process. When confronted with a surface with heterogeneous thermal and tactile inputs, the interactions at the sensory processing stream could result in sensations that deviate from physical reality, such as the illusory thermal uniformity in TR stimulation and the burning sensations in thermal grill illusion [49,50]. Not to mention, haptic estimates, such as temperature, weight, surface texture and size, can be influenced by visual inputs [9,10,11,12]. In developing multimodal haptic interfaces aimed at providing a holistic experience in telecommunication and virtual reality environments, it is thus important to understand how our brain processes and integrates multisensory information and to characterize the correspondence between physical inputs and the perceptual outcome in order to achieve optimal performance. By utilizing the properties of human perception, it is possible to provide a range haptic feedback that is wider than the capability of the haptic device. For example, based on TR, a thermally uniform surface can be created with discrete thermal stimulation and thermal feedback can be presented by a skin site free of contact with a thermal stimulator [13], and based on thermal grill illusion, the burning sensations created by interlacing innocuous warm and cold stimulation. In addition, the manipulation of object temperature, surface texture, size and weight can also be achieved by utilizing visual feedback.

6. Conclusion

In the present study, we showed that temperature integration under TR results from a simple averaging scheme (either Bayesian or linear), consistent with Bayesian cue combination processes found in other sensory dimensions. Further, we demonstrated that prolonged contact with TR stimulation resulted in adaptation to the local variations of veridical temperatures, indicating thermal adaptation occurs prior to thermal-tactile integration in TR. Our findings demonstrate that processing of haptic object perception is highly mediated, and rests on object inferences. This process facilitates object exploration and identification in our complicated natural environment. By demonstrating these commonalities with sensory processing across domains, our results present a new understanding of this essential aspect of experience and can serve as a basis for haptic display design.

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